

TROPICAL ALPINE ENVIRONMENTS

Plant form and function

Edited by

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1

Introduction to tropical alpine vegetation

ALAN P. SMITH

The general term 'tropical alpine' refers to regions within the tropics occurring between the upper limit of continuous, closed-canopy forest (often around 3500–3900 m) and the upper limit of plant life (often around 4600–4900 m: Hedberg 1951, 1964; Beaman 1962; Troll 1969; Wade & McVean 1969; Wardle 1971; Van der Hammen & Ruiz 1984; Vuilleumier & Monasterio 1986; see Figure 1.1) and is used in preference to regional terms such as '*páramo*' and '*jalca*' in the moist Andes from Venezuela to Northern Peru, '*puna*' in the drier central Andes, and 'Afroalpine' and 'moorland' in Africa. No clear lower boundary can be defined where natural timberline has been eliminated by man, as in many areas of the Andes and Papua New Guinea (Wade & McVean 1969; Hope 1976; Ellenberg 1979; Ruthsatz 1983), or where the forest is patchy or absent due to low rainfall, as on the north slope of Mount Kenya (Coe 1967; Figure 1.2) and the western slopes of the Peruvian Andes (Weberbauer 1911). In these cases alpine species merge gradually with species of montane pasture, savanna or desert.

Physiognomy of tropical alpine vegetation varies greatly with climatic and edaphic factors; however, certain trends are held in common by many New and Old World tropical alpine areas (see, for example, Hedberg 1964; Coe 1967; Cuatrecasas 1968; Wade & McVean 1969; J. Smith 1977, 1980; Cleef 1978), suggesting convergent evolution (Hedberg & Hedberg 1979; Halloy 1983; Smith & Young 1987).

Near the treeline, tussock grasses and erect shrubs with small leathery evergreen leaves often dominate the vegetation. With increasing elevation, tussock grasses and shrubs generally decrease in relative importance, and the vegetation is increasingly dominated by giant rosette plants (perennial, large-leaved rosettes, supported by unbranched or little-branched woody stems, with dead leaves typically retained on the stem for many years).

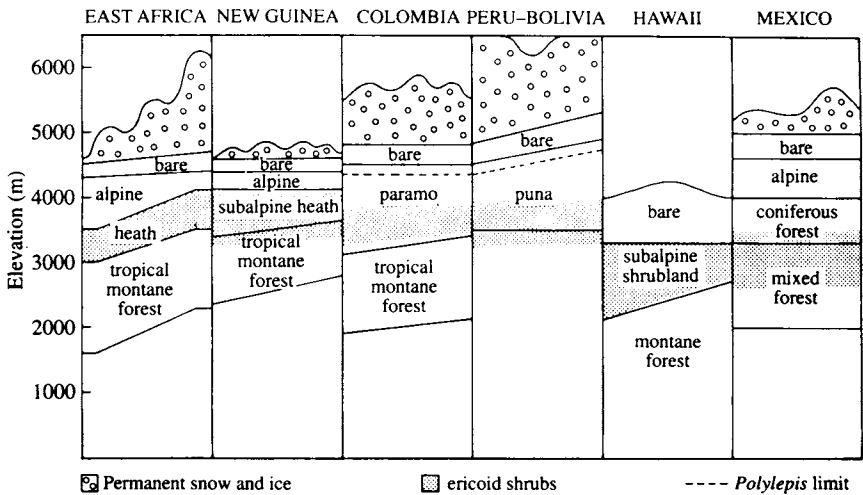


Figure 1.1. A diagrammatic summary of vegetation distribution on some New and Old World mountains. (Adapted from Troll 1968, Figure 16.)



Figure 1.2. Dry shrub-grass community on the north slope of Mount Kenya at 3300 m. Shrubs include *Helichrysum*, *Artemisia* and *Phillipia*. On slopes of Mount Kenya with higher rainfall, closed-canopy forest can occur at this elevation.



Figure 1.3. *Puya raimondii* (Bromeliaceae) at 4250 m, near Huancayo, Peru; individual at left is dispersing seeds.

Prostrate shrubs, non-tussock grasses and small perennial herbs are also common at intermediate elevations. Giant rosettes are by far the most characteristic aspect of tropical alpine vegetation, differentiating most of these communities from temperate alpine and arctic areas. The form has evolved repeatedly in the Andes (*Puya*, Bromeliaceae, Figure 1.3; *Espeletia*, Asteraceae, Figures 1.4–1.7; *Lupinus*, Leguminosae, Figure 1.8), Africa (*Senecio* and *Carduus*, Asteraceae; *Lobelia*, Campanulaceae, Figures 1.9–1.12), New Guinea (*Cyathea*, Figures 1.13 and 1.14), Hawaii (*Argyroxiphium*, Asteraceae, Figure 1.15) and the Canary Islands, just outside the Tropics (*Echium*, Boraginaceae, Figure 1.16). The growth form is absent from the dry volcanic peaks of Mexico, and from Mount Kinabalu (4101 m, lat. 6° N) in Borneo – a peak dominated by exposed rock. Giant rosettes



Figure 1.4. Venezuelan Andes (Mucubají). Lateral moraine at 3600 m, with dense stands of the giant rosette *Espeletia schultzei* (Asteraceae). Rosettes are interspersed with tussock grasses (mostly *Muehlenbeckia erectifolia*) and shrubs of *Hypericum*.

appear to play a particularly important role in the vegetation of the comparatively mesic alpine areas of Africa (Hedberg 1964; Coe 1967; Smith & Young 1982) and the northern Andes (Monasterio 1979; Smith 1981) where they can create 'savanna woodland' communities somewhat similar in physiognomy to palm savannas of the dry lowland tropics. These giant rosette communities should probably not be considered as merely extensions of montane forest into the alpine zone. In the northern Andes and on Mount Kenya giant rosettes are typically either absent or short in stature near treeline, and tend to increase in stature, both within and between species, with increasing elevation (A. Smith 1980), dramatically reversing the elevational trend seen in forest tree stature.

Isolated pockets of true closed canopy forest composed of *Polylepis* (Rosaceae) can occur well above the general treeline in the Andes at elevations up to 4300 m, typically occupying sheltered talus slopes (Figure 1.17). The presence of such forest pockets has led to speculation that forest may once have extended to far greater elevations than at present, but clear evidence is lacking (A. Smith 1977). Similar pockets of forest occur



Figure 1.5. A population of *Espeletia timotensis* (Asteraceae) at 4200 m, Piedras Blancas, Venezuela, with Dr José Cuatrecasas.

on Mount Wilhelm, Papua New Guinea at elevations of up to 3900 m (Wade & McVean 1969) and in this case probably are the result of human interference. Stands of the arborescent *Senecio keniodendron* (Asteraceae) on Mount Kenya can sometimes form a nearly closed canopy on mesic talus slopes at elevations of 4000–4200 m (Figure 1.18). The factors responsible for tropical treeline and for these isolated forest patches above treeline are in large part unknown (Walter & Medina 1969; Wardle 1971; A. Smith 1977).

Giant rosettes can extend to over 4600 m in Africa and to over 4500 m in the Andes, but are restricted to considerably lower elevations in other tropical alpine areas. At a given elevation, the relative importance of



Figure 1.6.

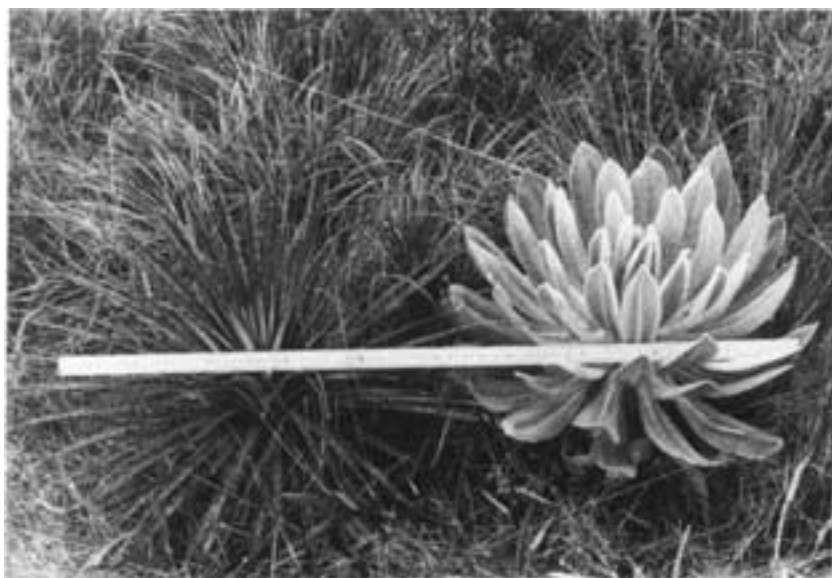


Figure 1.7.



Figure 1.8. *Lupinus alopecuroides* (Leguminosae), a monocarpic rosette species at 4150 m, Purace, Colombia.

tussock grasses versus giant rosettes generally shifts in favour of grasses as rainfall decreases; thus, the dry, fire-prone north slope of Mount Kenya and the analogous puna region of the central Andes have extensive cover by tussock grasses, with giant rosettes often restricted to comparatively rocky steep sites. Experimental studies on *Espeletia* in Venezuela suggest that tussock grasses can significantly reduce growth, reproduction and seedling establishment (Smith 1984). Fire is a major source of mortality both for *Espeletia* in the northern Andes (Smith 1981) and for *Senecio* on Mount Kenya (Smith & Young, Chapter 15).

At elevations above approximately 4200 m in the Andes and on Mount Kenya a combination of reduced rainfall and increased nocturnal soil frost heaving typically creates extensive areas of bare soil, resulting in 'alpine desert' (Monasterio 1979; Perez 1987a; see Figure 1.19). Extremely low rainfall can result in true alpine desert vegetation, as in parts of the

Figure 1.6. Purace, Colombian Andes. Foreground: *Espeletia hartwegiana* (Asteraceae) and scattered *Putia hamata* (Bromeliaceae) in a bog at 3400 m.

Figure 1.7. Purace, Colombian Andes at 3400 m; *Espeletia hartwegiana* (right) and *Puya hamata* (left).



Figure 1.9.



Figure 1.10.



Figure 1.11. Mount Kenya, 4250 m; *Carduus keniophyllum* (Asteraceae), a giant rosette species particularly common near hyrax colonies.

Peruvian and Bolivian Andes, where cactus species occur well above 4000 m (Weberbauer 1911; Herzog 1923).

Cushion plants can sometimes dominate the vegetation above 4000 m in the northern and central Andes, but appear to be less important in other tropical alpine areas (Rauh 1988). They may occur in desert-like puna habitats of both Peru and Bolivia (Weberbauer 1911; Hodge 1926) and in the moister páramo regions from northern Peru to Venezuela, where they appear to occur commonly on seepage slopes. The ecology of this growth form has been largely ignored in the tropics.

At the upper limit of plant life, low herbs, grasses and lichens dominate, and giant rosettes and shrubs generally drop out. The factors controlling the upper limit of plant life have not been analysed, although work has

Figure 1.9. Teleki Valey, Mount Kenya at 4200 m. A. *Lobelia telekii*, B. *Lobelia keniensis*, C. *Senecio brassica*, D. *Senecio keniodendron*. The dominant ground cover is *Alchemilla johnstonii*.

Figure 1.10. Teleki Valley, Mount Kenya. A topographic gradient spanning c. 4000–4150 m elevation, illustrating characteristic zonation of *Senecio brassica* (light-colored vegetation toward valley bottom) and *Senecio keniodendron* (upper slopes).



Figure 1.12.



Figure 1.13.



Figure 1.14. Mount Wilhelm, Pindaunde Valley, 3490 m; *Cyathea atrox*.

been done on *Draba chionophila* (Brassicaceae), one of the highest elevation species in the Venezuelan Andes (see Pfitsch, Chapter 8; also Perez 1987b). Glaciers are receding throughout the tropics, suggesting that plants may be colonizing progressively higher elevations (Coe 1967; Hastenrath 1985).

The tendency to divide tropical alpine areas into discrete elevational

Figure 1.12. Mount Elgon, 4000 m; a stand of *Senecio baratipes*, interspersed with tussock grasses and shrubs of *Helichrysum*.

Figure 1.13. Mount Wilhelm, Pindaunde Valley, Papua New Guinea, 3490 m. Treefern in foreground is *Cyathea gleichenoides*. Trees in background are primarily *Podocarpus compactus* (Podocarpaceae) and *Rapanea vaccinoides* (Myrtaceae).



Figure 1.15. Haleakala Crater, Maui, Hawaii, at 2180 m; *Argyroxiphium sandwicense* (Asteraceae).

zones (e.g. subpáramo, páramo, superpáramo; Cuatrecasas 1968; ericaceous zone, alpine zone: Hedberg 1964; see also Figure 1.1) appears to have little objective basis in actual community structure. Rather, communities appear to vary continuously along climatic and edaphic gradients, with few distinct discontinuities. However, very few quantitative data on spatial variation in community structure are available for tropical alpine areas (Hamilton & Perrott 1981; Baruch 1984).

Tropical alpine floras typically contain elements derived from the surrounding montane forests as well as from both South and North Temperate floras (Hedberg 1961; Clayton 1976; Cleef 1979; Smith 1982). Generic affinities with floras of temperate latitudes appear to increase



Figure 1.16. El Teide Volcano, Tenerife, Canary Islands, at 2100 m; *Echium wilprettii* (Boraginaceae) a subtropical monocarpic giant rosette species that converges on *Argyroxiphium*.

with increasing elevation (see, for example, Gadow 1907–1909; Wade & McVean 1969). Species richness is low compared to tropical lowland forest, but comparable to that for temperate alpine and arctic tundra communities (Wade & McVean 1969). There is no obvious latitudinal gradient in species richness among high mountain and tundra communities, at least on a local (‘alpha diversity’) scale (Hanselman 1975). This provides a striking contrast to the clear latitudinal gradient in local species richness found among lowland forest communities. There is great variability in taxonomic richness among tropical alpine communities. The alpine flora of the northern Andes is much richer (over 300 genera) than



Figure 1.17.



Figure 1.18.



Figure 1.19. Mount Kenya, Hobley Valley at approximately 4500 m, illustrating 'alpine desert'.

the floras of the smaller and more fragmented alpine areas of Africa (103 genera) and Papua New Guinea (107 genera) (Cleef 1979). Simpson (1974) demonstrated that variation in floristic richness from region to region within the northern Andes is positive correlated with habitat area; she also suggested that variations in habitat area and isolation during and

Figure 1.17. Venezuelan Andes, 4100 m; an isolated patch of closed-canopy *Polyepis sericea* (Rosaceae) forest on a talus slope. In foreground, *Espeletia moritziana* interspersed with shrubs of *Hypericum* and *Arcytophyllum*.

Figure 1.18. Mount Kenya, Teleki Valley, 4200 m; a closed-canopy stand of *Senecio keniodendron* on a talus slope. The tussock grassland in the foreground occurs on mineral soil.

since the Pleistocene may have influenced current patterns of species richness (see also Hooghiemstra 1984). Janzen (1967) has suggested that there is less environmental overlap between the top and bottom of elevational gradients on tropical mountains than between the top and bottom of temperate latitude gradients with similar elevational ranges. This could result in decreased gene flow along tropical gradients, potentially facilitating speciation. A. Smith (1975) and Huey (1978) present data consistent with the hypothesis.

Plant growth rates appear to be generally low in tropical alpine areas, although few data are available (Hedberg 1969; Sturm 1978; Beck *et al.* 1980; A. Smith 1980, 1981; Smith & Young, 1982; Young, Chapter 14). Growth rates appear to be reduced by dry season drought stress, especially during unusually dry years (Smith 1981) and by both intra- and inter-specific competition (A. Smith 1980, 1984).

Herbivory appears to be an important influence on plant population biology and plant community structure on Mount Kenya (Young and Smith, Chapter 18). Few data are available for the Andes; herbivory on *Espeletia schultzei* in Venezuela appears to be extensive only near the lower limit on its range (A. Smith 1980); tussock grasses and herbs are commonly browsed by rabbits and small rodents in the Venezuelan Andes (A. P. Smith, personal observations); herbivory by larger mammals such as deer, mountain tapir and vicuña has been greatly reduced by hunting (Kofford 1957).

Rates of succession in tropical alpine communities appear to be low (Janzen 1973). An experimental study in the Venezuelan Andes (W. Pfitsch and A. Smith, unpublished data) suggest that at comparatively low elevations (3100 m) succession on bare soil involves invasion by early successional specialist species, which disappear later in succession and are replaced by late successional specialists. Early successional specialists decline in importance with increasing elevation: at 4200 m succession takes the form of a gradual accumulation of species which persist in mature community. At and above 3500 m succession can be greatly slowed by soil frost heaving and erosion, which eliminate seedlings before they can get established. At 3600 m several 4 m quadrats which were cleared of vegetation in 1973 were still bare in 1984 (W. Pfitsch and A. Smith, unpublished data) suggesting that higher elevation communities on tropical mountains can be quite fragile (cf. Ruthsatz 1983).

The ratio of aboveground to belowground biomass appears to be unusually high in tropical alpine areas: 10:1 in alpine grassland of Papua New Guinea (Hnatiuk 1878) and 2.5:1 to 1:1 for the Venezuelan Andes

(Smith & Klinger 1985). These values are higher than those found for arctic and temperate alpine communities (Smith & Klinger 1985), and may reflect both the absence of large underground storage organs and the more extensive development of aboveground support tissues in many tropical alpine plants. Extensive data on nutrient cycles, hydrology, energy flow and trophic structure are not available for tropical alpine sites (see Rehder, this volume and Korner 1989); tropical alpine 'ecosystems' thus remain poorly known, despite much quantitative information on component species.

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